

Use of habitat by mammals in eastern Australian forests: are common species important in forest management?

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ABSTRACT

Censuses were taken of three common species of small mammals at forest sites in four regions in the Australian Capital Territory and New South Wales. Numbers of Agile Antechinus *Antechinus agilis* were best predicted by indices of abundance of tree hollows and invertebrate food resources, whereas numbers of Brown Antechinus *Antechinus stuartii* were associated most consistently with tree hollows and then numbers of logs and coexisting Bush Rats *Rattus fuscipes*. Rats were not associated consistently with any single habitat components, but generally favoured sites of high vegetation density with litter or logs providing ground-level cover. *Rattus fuscipes* was the only species to show a difference in abundance between forest types, being 2.6 times more numerous in tall open-forest than open-forest in one study area. Radio-tracking confirmed that the habitat components most strongly associated with the local abundance of *A. stuartii* and *R. fuscipes* were used as day time shelters by each species.

Because the three study species are common in forest environments in eastern Australia, they are not considered important from perspectives of conservation or management. However, in local areas where common species reach high numbers, they will be more important in controlling energy, nutrient and resource flows than rare species, and are more likely to be involved in interaction webs and co-evolutionary relationships with suites of other species. The tree hollows, logs and other habitat components associated with high local abundances of our common study species are also components required by many less common and threatened species of vertebrates. In view of these observations, we suggest that 'hot spots' of common species may act as uniquely important indices of local resource and species richness, and thus of local forest quality. An exciting and profitable line of research would be to compare the performance of a 'common species index' with more traditional measures of forest quality such as presence of threatened species, species richness or structure-based indicators.

Key words: *Antechinus*, *Rattus*, habitat use, tree hollows, common species, indicator species, wildlife management

Introduction

Attitudes to the management of forest fauna have varied greatly in Australia since European settlement, particularly over the last several decades. In the early part of the twentieth century, wildlife management often took the form of exploitation for the fur and meat industries (Frawley and Semple 1988); during times of economic depression, culls of Brushtail Possums, Koalas and other marsupials were carried out to alleviate unemployment (Warneke 1978; Facey 1981). During the same period, many species of large and medium-sized marsupials were controlled when they ventured from forest edges into surrounding pastures (Hrdina 1997), while deer and other game species were hunted for sport (Rolls 1969). These activities took place against a backdrop of forest loss and fragmentation in many areas (Lunney 1991a; Reed 1991).

By the mid twentieth century there was concern that many species of native forest vertebrates were declining (Troughton 1957; Marlow 1958), and by 1973 Frith (1973, p9) concluded that "The arrival of Europeans was of great significance to the native fauna.....Their effect (..and that of many exotic carnivorous and herbivorous birds and mammals..) has been profound and uniformly disastrous".

Interest in the management of forest wildlife has surged over the last 30 years (e.g. Tyndale-Biscoe and Calaby 1975; Recher *et al.* 1980; Lunney 1991b, 2004; Lindenmayer and Franklin 2002). Most States and Territories in Australia now have policies that seek to maintain sustainable forest industries, and all have developed lists of threatened biota that are afforded legislative protection. The *Environment Protection and Biodiversity Conservation Act 1999* allows for listing at the Commonwealth level. In addition to the construction of statutory instruments, much research has been carried out on the habitat requirements of forest vertebrates, especially taxa that are forest-dependent or listed as threatened. The focus on such 'special species' (*sensu* Hunter 1990) has allowed identification of taxa that require old growth and other types of forest, and that need particular food or shelter resources such as tree hollows (e.g. Kavanagh 1991; Recher 1996; McComb and Lindenmayer 1999; Gibbons and Lindenmayer 2002). Such research findings are crucial for informed and effective management.

In contrast to the attention given to threatened taxa, common species are often overlooked in inventories of

forest fauna, and prescriptions are seldom developed to conserve them during forestry operations. However, there are several reasons why common species should warrant some attention. Firstly, 'commonness' is not an immutable attribute of any species; even abundant taxa may decline quickly and become locally extinct if habitat is degraded or conditions generally become unsuitable. The Grey-headed Flying-fox *Pteropus poliocephalus* provides a good example (Eby and Lunney 2002). If such species can be identified during the initial stages of decline, management for conservation should be more cost-effective (Possingham *et al.* 2002; Lamoreux *et al.* 2003). Secondly, because common species are usually abundant in at least some parts of their ranges, it is easier to identify habitat and resource components that they require and to construct predictive models of their abundance. This allows for informed judgements about how timber harvesting, thinning or other forestry operations may affect them. Thirdly, common species may act as 'surrogates' for threatened taxa (Ferrier and Watson 1997). For example, locally high densities of Ringtail Possums *Pseudocheirus peregrinus* and gliders may facilitate populations of Powerful Owls *Ninox strenua* and Sooty Owls *Tyto tenebricosa* (Kavanagh 1991; Milledge *et al.* 1991), while Spotted-tailed Quolls *Dasyurus maculatus* often occur where medium-sized marsupial prey are numerous (A. Glen, University of Sydney, pers. comm. 2003).

In this chapter, we investigate the habitat use of three species of small mammals that occur commonly in forest environments in eastern Australia, and attempt to identify the habitat components that are most strongly associated with the species' abundances. We then discuss the implications of our results for forest management, considering in particular the importance of common species in the management process.

Methods

Study species

The three study species were the Brown Antechinus *Antechinus stuartii* (~30 g), the Agile Antechinus *Antechinus agilis* (~25 g), and the Bush Rat *Rattus fuscipes* (~100 g) (Figs 1-3). The two species of *Antechinus* occur broadly in heath and timbered environments in eastern Australia, with higher numbers being recorded in wetter and more productive forests than in open forest and woodland (Barnett *et al.* 1978; Dickman 1980; Hall and Lee 1982; Statham and Harden 1982; Wilson *et al.* 1986; Catling and Burt 1995; Tasker and Dickman 2004). The habitat preferences of these species do not always appear to be consistent; although this may be due in part to the recent recognition that *A. agilis* and *A. stuartii* are separate species (Dickman *et al.* 1998) with potentially different habitat requirements, some variation in habitat use still occurs within each species in different sites at different times (Statham and Harden 1982; Dickman *et al.* 1983; Moro 1991; Cox *et al.* 2003). *Rattus fuscipes* also occurs abundantly in wet forest and heath, but is sparse or absent in open woodland and habitats lacking ground cover (Warneke 1971; Braithwaite *et al.* 1978; Hall and Lee 1982; Moro 1991, Twyford 1997; Maitz and Dickman 2001). Although its preference for cover at ground level is



Figure 1. Brown Antechinus *Antechinus stuartii* with the senior author during this study in 1990. (Photo: Malcolm Ricketts)

usually consistent, *R. fuscipes* nonetheless shifts its use of logs, stems, litter and other habitat components between times and locations (Statham and Harden 1982). All three species can persist in fragmented forest environments (Knight and Fox 2000; Lindenmayer *et al.* 2001; Cox *et al.* 2003), but seldom survive in small patches (< 100 ha) in suburban areas (Dickman 1996).

Study areas

Fieldwork was carried out in four areas at different times:

1. Brindabella Range, Australian Capital Territory (approximate centre of study area: 35° 21' S, 148° 50' E). Lying just to the south west of Canberra, the Brindabellas form part of the Great Dividing Range, and are characterized by rugged topography dissected by first and second order streams. Rainfall averages from 654 mm a year at lower elevations to over 1000 mm in the ranges; average winter minima are 0.9°C and summer maxima are 27.4°C (Bureau of Meteorology 1988). Mixed open-forest dominated by broad-leaved peppermint *Eucalyptus dives*, red stringybark *E. macrorhyncha*, messmate *E. robertsonii* and narrow-leaved peppermint *E. radiata* occurs on slopes below 1200 m, with ribbon gum *E. viminalis* and brown barrel *E. fastigata* occurring along wet valley floors; above 1200 m, mountain gum *E. dalyrpleana* and alpine ash *E. delegatensis* become dominant (Dickman *et al.* 1983). Open-forest on the lower slopes of the Brindabella Range has been extensively cleared or modified for pastoral activity; tall timber has been selectively removed from much of the range, or clear-felled and replaced by plantations of the exotic *Pinus radiata*. The fire history of the area has been poorly documented, but we saw little evidence of recent



Figure 2. Agile Antechinus *Antechinus agilis*. (Photo: Chris Dickman)



Figure 3. Bush Rat *Rattus fuscipes*. (Photo: Chris Dickman)

fires at any sites. Study sites containing populations of *A. agilis* and *R. fuscipes* were established in the Brindabella Range and in undulating country immediately to the north (Dickman 1980), and sampled predominantly from March to August from 1978 to 1981.

2. Ku-ring-gai Chase National Park, New South Wales (33° 40' S, 151° 10' E). This National Park, lying on the northern outskirts of Sydney, comprises 14 656 ha of rugged sandstone country characterized by deeply eroded valleys and extensive waterways. The climate is temperate, with a mean annual rainfall of 1212 mm and average temperature minima and maxima, respectively, of 7.9°C and 25.7°C (Bureau of Meteorology 1988). The Park supports a broad range of vegetation communities, including closed forest, open and tall open-forest, woodland, heath and sedgeland (Thomas and Benson 1985; Benson and Howell 1990), with Sydney blue gum *Eucalyptus saligna* and blackbutt *E. pilularis* dominating forest communities and scribbly gum *E. haemastoma*, red bloodwood *E. gummifera*, the apples *Angophora costata* and *A. hispida* and *Banksia ericifolia* the woodlands and heaths (Bradford 1976).

Ku-ring-gai has been subjected to little or no logging activity, but experiences frequent fires. This area contained populations of *A. stuartii* and *R. fuscipes*, and was sampled between March and August 1990.

3. Chichester National Park, New South Wales (32° 08' S, 151° 44' E). This study area lies on the southern escarpment of the Barrington Tops plateau, north of Dungog. The topography is dominated by high ridges, steep slopes and creeks that run to the south and south-east. Rainfall at Dungog is 983 mm a year, while average minimum and maximum temperatures are 3.6°C and 29.2°C, respectively (Bureau of Meteorology 1988). Forest in the Chichester region was selectively logged for red cedar *Toona australis* from the 1820s to around 1900, and has been subject to general hardwood harvesting since the 1900s (Fraser and Vickery 1937). The vegetation is tall open-forest dominated by Sydney blue gum *E. saligna* and silvertop stringybark *E. laevopinea*, although significant areas of closed forest dominated by Antarctic beech *Nothofagus moorei* occur at elevations >1000 m. State Forests of NSW transferred part of Chichester State Forest to the NSW National Parks and Wildlife Service (now Department of Environment and Conservation) in 1998, but retain jurisdiction over several catchments that had been subjected to experimental harvesting (the Karuah catchments, Cornish 1993), and in which we established eight sampling sites (Steeves 1990). Intensive sampling was carried out in July 1990, and sporadic sampling in July 1991, July 1992 and May 1993. *Antechinus stuartii* and *R. fuscipes* were found in this area.
4. Blue Mountains National Park, New South Wales (33° 38' S, 150° 18' E). The Blue Mountains form the western edge of the Sydney Basin. In the region around Blackheath, where sampling was focused, the landscape comprises deeply-incised sandstone gullies that support open and tall open-forest with a dense understorey of ferns and shrubs. Dominant tree species include brittle gum *E. mannifera*, *E. sclerophylla* and *E. stricta*; understorey species include *Hakea teretifolia*, *Banksia* and *Leptospermum* spp. (Banks and Dickman 2000;

Maitz and Dickman 2001). Three sampling sites within this area had been burnt two years before and a further four had been burnt five years previously; all other sites appeared to be long-unburnt. Seasonal temperatures fluctuate markedly, from mean minima in July of 1.6°C to maxima of 22.9°C in January, while mean annual rainfall is 1342 mm (Bureau of Meteorology 1988). Sampling was carried out between March and August 1994. This area supported populations of *A. stuartii* and *R. fuscipes*.

Trapping and tracking methods

Sampling in each of the four study areas was carried out with slightly different objectives and under different constraints, hence trapping and tracking methods and assessments of habitat varied. In all areas, small mammals were live-trapped using Elliott aluminium box traps (33 x 10 x 10 cm) using standard trap setting and baiting procedures (Tasker and Dickman 2002). At areas 1 and 2, above, traps were set at intervals of 15-20 m on grids of 7 x 7 traps covering 0.81-1.44 ha. Thirty-seven independent grids were established in the Brindabella Range and 24 at Ku-ring-gai, with independence being ensured by spatial separation (57 grids were >3 km apart) or physical barriers (two pairs of grids at Ku-ring-gai were 100 m apart, separated by a bitumen road). In each of the Chichester and Blue Mountains study areas, 15 transect lines were established with 25 traps set per line at intervals of 10 m. Separation between lines was >1 km. In all areas, we attempted to ensure that all major forest types, fire and management regimes (as described in *Study Areas*, above) were sampled. Except for five grids at Ku-ring-gai (see *Analyses of Data*, below), all sites were trapped once only to avoid problems of dependency in the dataset.

Animals were live-trapped for four consecutive nights at all sites, with trap checks carried out near dawn. Individuals were identified, weighed, marked, inspected for sex and reproductive condition, and most were then released immediately. However, a few individuals were equipped with a radio-collar prior to release to investigate their use of habitat and nest sites. Tags were single-stage transmitters with 5-7 cm whip antennae, weighing ≤ 1.5 g, supplied by Biotrack (Wareham, UK) or Titley Electronics (Ballina, Australia). Collared animals were held either in a bag for up to two hours or in a cage throughout the day to check the fit of the collar, and then released at the point of capture. Up to four fixes were obtained on individuals by night, and 1-2 by day, using Telonics TR2 receivers and hand-held H-frame antennae. In this study we present results only for day locations because we could walk to find the precise positions of collared animals; night fixes, obtained by triangulation, were subject to greater error and hence did not provide reliable information on habitat use.

Habitat assessments

We assessed habitat at two scales to investigate whether the study species responded differently to them. Firstly, we assigned the grids or trapping transects in each area to a dominant vegetation category, based on the structural classification of Specht (1970). Usually grids and lines fell entirely within a single vegetation category and were easy to classify; four trapping transects traversed 2-3 categories, and these were ignored in subsequent analyses.

Secondly, we measured a series of habitat components and other factors that previous studies and our own radio-tracking results suggested may be related to the abundance of the three study species. These components (and variable codes used in later analyses) were:

1. *Vegetation density*. (VEG). In three study areas, indices of above-ground vegetation density were derived using a 2 cm diameter pole calibrated into four height classes; 0-25 cm (VEGA), 26-50 cm (VEGB), 51-100 cm (VEGC), and 101-150 cm (VEGD). With the pole held vertically, vegetation touching the pole was counted in each of the four height intervals. In the Brindabella study area, vegetation density was assessed similarly, but only at 0-100 cm (VEGE) and 101-150 cm. Assessments were made within 1 m of each trap on transect lines and at 21 randomly-selected points on grids, and counts averaged for each height class per site. The average total number of vegetation strikes (VEGTOT) was also calculated for each site to produce an overall index of vegetation density.
2. *Leaf litter*. (LITTER). Litter depth was recorded at 21 randomly-selected points on grids and within 1 m of traps on transect lines, and values averaged to obtain mean litter depth per site. Care was taken to avoid any areas of litter that we had previously disturbed.
3. *Rock cover*. (ROCK). Crevices in rocks potentially provide cover for the study species (Fairley 1976; Whelan *et al.* 1996), and thus were evaluated here. We used the seven lines of traps on grids and alternate groups of five traps on trap lines as belt transects, and scored rock crevices on a scale of 0-10 per transect, with 0 = no crevices and 10 = abundant crevices. Ranks were used because we could not confidently count available crevices. Assessments were made up to 5 m either side of the transect. Scores were averaged across transects to obtain an index of rock cover within each site.
4. *Logs*. (LOG). Defined as fallen trees or segments of trees >10 cm diameter and >100 cm long, logs were counted on the same transects used for rock cover and the total number used as an index of log availability.
5. *Tree hollows*. (HOLLOW). As it was not possible to count hollows directly, we assumed that hollow density would be a function of the numbers of trees and stags present at a site multiplied by the average number of hollows per tree. To estimate this average, we initially searched freshly fallen trees at each site and attempted to count all potential hollows. Because hollows under the trees were not visible, we multiplied the number of hollows observed by 1.1 to 1.5, depending on the area of the underside of the tree that was obscured, to obtain an approximate total number of hollows. For 14 fallen trees searched in this way, we estimated 1-39 hollows. Unfortunately, numbers of hollows varied inconsistently with tree species, apparent age, height, degree of branching, disease status and other factors, making it difficult to reliably predict numbers of hollows in standing trees. Thus, we derived a simple tree hollow index by tallying trees and stags >8 m high on the

same transects as used for rock cover, and multiplying by two the number of very large (>25 m high) or old trees that were present. This was expected to yield a very conservative estimate of the true availability of hollows. The difficulties of surveying hollows in forest trees, especially for small mammals, have been outlined by Gibbons and Lindenmayer (2002).

6. *Water*. (WATER). Running creeks, seepages, still water and dry creek beds were counted at each site to provide an index of availability of fresh water. All water sources were counted within the confines of grids and within 10 m either side of the transect lines.
7. *Years since fire*. (FIRE). This was assessed for the Ku-ring-gai and Blue Mountains study areas using NSW National Parks and Wildlife Service fire maps. These showed that fires had occurred 1-17 years prior to sampling. Fire histories were not available for the other study areas. However, with the exception of four of the Karuah catchment sites that had been burnt following experimental harvesting 7 years previously, there was little evidence that any sites had burnt recently. Fire history was therefore disregarded for the Brindabella and Chichester study areas.
8. *Years since logging*. (LOGGING). This was evaluated for the Brindabella and Chichester sites by discussion with personnel from the ACT Department of Conservation and State Forests of NSW, respectively. At most sites, if logging had taken place, it had been aimed at selective removal of large trees. However, four sites at Chichester had been subject to 50% canopy reduction and two more had been clear-felled some 7 years before. No significant logging had taken place in either the Blue Mountains or Ku-ring-gai National Parks.
9. *Habitat disturbance*. (DIST). Four types of disturbance were recognized and scored if they occurred within 10 m of a grid or trapping transect. These were picnic area (score = 1.0), bitumen road on site boundary (1.0), unsealed vehicular track on site boundary (0.5), and walking track within site (0.5). Scores were summed to provide an overall index of habitat disturbance for each site.
10. *Aspect* (ASP) and *altitude* (ALT). These were established for each site using topographic maps.
11. *Abundance of food*. (FOOD). All the study species eat invertebrates; the two species of *Antechinus* are specialist insectivores, while *R. fuscipes* takes invertebrates opportunistically (Warneke 1971; Statham 1982; Fox and Archer 1984; Dickman 1986a; Lunney *et al.* 2001). Pitfall traps were used to sample invertebrates, and consisted of plastic cups (4 cm diameter, 6 cm deep, half filled with 3% formalin) buried flush in soil and leaf litter in each site. One pitfall trap was set within 2 m of each Elliott trap on grids, and 30 pitfalls were set 1-2 m apart midway along trapping transects. Pitfall traps were set for four nights, then removed. Invertebrates ≥ 3.0 mm were counted and oven dried, and the data expressed as mean numbers (FOODNO) and dry biomass

(FOODMASS), respectively, per pitfall trap per site. We discarded invertebrates <3.0 mm long because they are eaten rarely by any of the study species.

12. *Other species*. (SPECIES). To evaluate possible associations among the study species, estimates of species' numbers were made at each site and used as variables (*Antechinus* spp. = ANT; *R. fuscipes* = RAT) in further analyses.

Analyses of data

Animal numbers

The trapping data from each site were used to calculate minimum numbers known to be alive (KTBA), and also to derive estimates of numbers using Petersen and Jolly-Seber models (Krebs 1989). Exploratory analyses comparing estimates from each method on the Chichester dataset suggested that habitat associations were revealed more reliably using KTBA estimates because greater variance in the model estimates reduced statistical power to detect associations (Bausell and Li 2002). In addition, because there was evidence that some assumptions underpinning the population models were not met (in particular, trappability was often not equal), we used KTBA estimates throughout.

In further exploratory analyses, we compared KTBA estimates made at different times (March-April versus June-July) on the same five grids at Ku-ring-gai to determine whether populations of the study species were likely to be stable over the main period of sampling in autumn and winter. In a further attempt to evaluate seasonal variation in population sizes, KTBA data for Ku-ring-gai were divided into three time periods (eight grids sampled in each of March to mid-April, mid-April to mid-May, and mid-May to June) and compared. After Cochran's test confirmed homogeneity of variances, analysis of variance (anova) was used to compare KTBA estimates in both cases.

Habitat associations

Use of different categories of dominant vegetation by the study species was evaluated separately for each study area by comparing numbers KTBA in replicate grid or trapping transect sites in different vegetation types. Comparisons used anova, after Cochran's test indicated that variances were homogeneous.

Use of habitat components and other factors was also assessed separately for each study area, using both trapping (KTBA) and radio-tracking data. The numbers of each species KTBA were used as dependent variables in stepwise multiple linear regression models, with the habitat components as independent variables. To find the best fit for the data, and to check for normality and homoscedasticity (Marzluff 1984), simple linear regressions were computed initially of KTBA for each species against each of the microhabitat variables. The residuals in each regression were then examined and, to improve linearity, $\log_{10}(x+1)$ transformations were made on all variables.

To reduce the large number of independent variables prior to model building (Tabachnick and Fidell 1996), we first inspected the scatter in each habitat component and

discarded any that were relatively invariant. The variable-deletion procedure of Kendall (1980) was also employed to remove variables that were highly correlated with others. Forward and backward selection models were used; as outputs were similar, only the results of forward models are presented. Mallows's C_p statistic was used to determine the model of best fit (Quinn and Keough 2002), and product-moment correlations were computed to detect any further univariate associations. To further explore habitat associations, habitat component variables were standardized and then subjected to principal components analysis (PCA) to create a smaller number of uncorrelated component variables. Varimax rotation was used to maximize the variation in the original variables accounted for in the new PCA variables. These were then used in multiple regressions, as above. The new variables were interpreted by inspection of the factor loadings on the original raw variables (Tabachnick and Fidell 1996). Comparison of the PCA regressions with the stepwise models suggested that the PCA approach added little further insight into the pattern of habitat use of the study species; hence PCA results are not shown here, but can be found for the first three study areas in Steeves (1990). Concordance of the PCA and stepwise model results also provides confidence that the stepwise models were robust, despite the large numbers of independent variables that were entered.

The positions of radio-tracked animals were scored according to microhabitats 1-5 defined above. Variables 6-10 were not scored because they were unlikely to be independent of capture location; for example, an animal captured in a 10-year old burnt site at a certain altitude would likely be tracked there later, unless it made a very long range movement. Because relatively few animals were tracked successfully, results are presented simply as percentages of fixes obtained in each microhabitat.

Results

Animal numbers

In total, we captured 273 *Antechinus agilis*, 206 *A. stuartii*, and 817 *Rattus fuscipes* across the four study areas. No marked individuals were recorded moving between sites within areas, confirming that sites were independent. At Ku-ring-gai, numbers of animals known to be alive on the same five grids in March-April (*A. stuartii*: 4.2 animals per grid \pm 1.3 SE; *R. fuscipes*: 10.8 \pm 1.3 SE) were no different from those present in June-July (*A. stuartii*: 3.3 \pm 0.8 SE; *R. fuscipes*: 9.3 \pm 0.9 SE) (F values were 0.71 and 0.98, respectively; P ns for both). Numbers on eight different grids sampled at three different times were also similar for both species (*A. stuartii* varied from 2.6 \pm 0.7 to 3.9 \pm 1.8 SE animals per grid; F = 0.56, P ns; *R. fuscipes* from 8.0 \pm 2.0 to 10.6 \pm 1.8 SE animals per grid; F = 0.64, P ns). These results show that, for the autumn and winter period when most sampling was carried out, populations of both species could be considered to be stable.

Antechinus agilis

This species was captured at all 37 sites sampled in the Brindabella Range, with 1-26 individuals occurring per site.

Antechinus stuartii

At Ku-ring-gai, 70 individuals were captured in 19 of the 24 sites, with captures ranging from 0-13 per site. At Chichester, only two sites failed to capture *A. stuartii*, with a total of 61 animals captured 0-10 times per site. All sites in the Blue Mountains were successfully sampled for this species, with 75 individuals captured 1-15 times.

Rattus fuscipes

This species was ubiquitous and abundant across the four study areas. A total of 469 individuals was captured in the Brindabellas (0-31 per site, 33 of 37 sites contained rats), 222 at Ku-ring-gai (1-16 animals per site), 46 at Chichester (0-6 per site, 13 of 15 sites contained rats), and 80 in the Blue Mountains (1-12 per site).

Habitat associations

Dominant vegetation categories

In the Brindabella Range, comparisons of abundance were made for animals sampled on grids in open-forest and tall open-forest. There was no difference in the numbers of *A. agilis* between these habitats (F = 1.78, P ns), but *R. fuscipes* was 2.6 times more numerous in tall open-forest (F = 3.94, P < 0.05). Comparisons of numbers of *A. stuartii* and *R. fuscipes* among closed-scrub, scrub-heath, low woodland, low open-woodland, burnt and unburnt habitats at Ku-ring-gai, among closed-forest, tall open-forest, logged and unlogged forest at Chichester and among open-forest, tall open-forest, burnt and unburnt habitats in the Blue Mountains failed to find any differences (F values ranged from 0.23-2.89, P ns for all).

Habitat components

For *A. agilis*, the index of tree hollows and numbers of pitfall-trapped invertebrates accounted for 75% of the variation in numbers between sites (Table 1). Correlations indicated some association between *A. agilis* and logs (r = +0.554, P < 0.001), vegetation density below 1m (r = +0.506, P < 0.01), numbers of *R. fuscipes* (r = +0.548, P < 0.001) and altitude (r = -0.357, P < 0.05), but these did not add significantly to the fit of the overall model.

For *A. stuartii*, regressions accounted for 41% to 59% of the variation in numbers across three study areas (Table 1). In all three areas, tree hollows emerged as important predictors of abundance; at Ku-ring-gai, numbers of *R. fuscipes* also entered the regression model, while in the Blue Mountains numbers of logs were important. Correlations were found between the numbers of *A. stuartii* and *R. fuscipes* in the Chichester study area (r = +0.601, P < 0.05) and between *A. stuartii* and numbers of pitfall-trapped invertebrates in the Blue Mountains (r = +0.683, P < 0.01), but these again failed to improve the fit of the models.

There was less consistency in variables associated with the abundance of *R. fuscipes*, with density of vegetation under 1 m, amount of litter, disturbance, numbers of logs, hollows and invertebrates contributing variably to regression models across the four study areas (Table 1). In addition, several variables were correlated with rat abundance in each study area but were not incorporated into the final models. In the

Brindabella Range these were tree hollows ($r = +0.527$, $P < 0.001$), rock cover ($r = -0.426$, $P < 0.01$), vegetation density over 1 m ($r = -0.545$, $P < 0.001$), depth of leaf litter ($r = +0.442$, $P < 0.01$), and numbers of *A. agilis* ($r = +0.548$, $P < 0.001$); at Ku-ring-gai, the numbers of *A. stuartii* were a correlate ($r = +0.480$, $P < 0.05$); at Chichester numbers of *A. stuartii* were a correlate ($r = +0.601$, $P < 0.05$); and in the Blue Mountains, correlates were vegetation density 51-100 cm above ground ($r = +0.553$, $P < 0.05$) and availability of water ($r = +0.529$, $P < 0.05$).

Animals were radio-tracked successfully in the Blue Mountains and Chichester National Parks, but not in the Brindabellas or Ku-ring-gai Chase National Park. In general, *A. stuartii* used hollows in trees and logs for shelter, with little use being made of vegetation, leaf litter or rock crevices (Table 2). Shelters in tree hollows were 2-24 m above ground, with 24 of 26 radio-locations being made in mature trees. *Rattus fuscipes* sheltered predominantly in logs, but made extensive use also of vegetation and banks of soil. Four of 23 radio-locations were made in hollows in stags 0.3-

Table 1. Relationships between the abundance of *Antechinus agilis*, *A. stuartii* and *Rattus fuscipes* and habitat component and other environmental variables in four study areas. Abundance (y) is expressed as numbers known to be alive.

Study area	Regression equation	R ²	F
<i>Antechinus agilis</i>			
Brindabellas ¹	$y = 0.445 + 0.458 (0.182)$ (HOLLOW) + $0.224 (0.589)$ (FOODNO)	0.754	51.99***
<i>Antechinus stuartii</i>			
Ku-ring-gai ²	$y = 1.119 + 0.451 (0.193)$ (HOLLOW) + $0.323 (0.210)$ (RAT)	0.409	7.27*
Chichester ³	$y = -0.819 + 0.732 (0.158)$ (HOLLOW)	0.536	15.00**
Blue Mountains ⁴	$y = 1.673 + 0.395 (0.138)$ (LOG) + + $0.639 (0.203)$ (HOLLOW)	0.592	11.31**
<i>Rattus fuscipes</i>			
Brindabellas ¹	$y = -3.066 + 0.833 (0.956)$ (VEGE) + 0.174 (1.489) (LOG)	0.767	55.89***
Ku-ring-gai ²	$y = 2.249 - 0.671 (1.227)$ (VEGA) - 0.310 (0.159) (HOLLOW) + $0.318 (0.309)$ (DIST)	0.481	6.19*
Chichester ³	$y = -0.588 + 0.713 (0.076)$ (HOLLOW) + $0.357(0.263)$ (FOODNO)	0.622	9.89**
Blue Mountains ⁵	$y = 1.781 + 0.968 (0.347)$ (LOG) + $0.063 (0.041)$ (LITTER) + $0.618 (0.125)$ (VEGB)	0.805	27.14***

Notes: Prior to regression analysis, the following were deleted: ¹WATER, DIST, ASP and FOODMASS; ²LOG, ALT, FOODNO and FOODMASS; ³ROCK, DIST; ⁴VEGA, ALT, FOODMASS, RAT; ⁵VEGA, ALT, FOODMASS, ANT. Codes for variables are given in the text; italics show standard errors of regression coefficients; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2. Habitat components used by *Antechinus stuartii* and *Rattus fuscipes* in the Blue Mountains and Chichester National Parks. Data are shown as percentages of radio-locations made by day on individuals in five habitat categories. Sample size, n , indicates the number of individuals tracked and in brackets the total numbers of radio-fixes obtained.

Study area	n	% of radio-locations in:				
		Vegetation	Leaf litter	Rock crevices	Logs	Hollows
<i>Antechinus stuartii</i>						
Blue Mts	8(27)	3.7	0.0	7.4	18.5	70.3
Chichester	4(8)	0.0	0.0	0.0	12.5	87.5
<i>Rattus fuscipes</i>						
Blue Mts	5(23)	30.4*	4.3	4.3	43.5	17.4

Notes: *Animals used above-ground vegetation and holes in banks of bare or sparsely covered soil above creeks.

2.6 m above ground level; no rats were recorded sheltering above ground in living trees. These components of habitat reflect those identified as important in the regression analyses, above.

Discussion

Patterns of abundance and habitat use

The two species of *Antechinus* and *Rattus fuscipes* were widespread and abundant in the four areas studied, with numbers at Ku-ring-gai remaining stable over the sampling period in autumn and winter. In each species, juveniles enter the trappable populations over summer and numbers usually are steady until declines in food resources drive populations to lower levels in winter and spring (Wood 1971; Wilson *et al.* 1986; Dickman 1989; Banks and Dickman 2000). By concentrating on trapping from March to August, we avoided sampling population troughs and hence obtained datasets that were relatively unbiased by seasonal demographic shifts.

There was little evidence of spatial variation in species' abundances among different categories of vegetation. With the exception of *R. fuscipes* in the Brindabella Range, the three species were distributed consistently among vegetation types and showed little variation in numbers between any of the types sampled (cf. Statham and Harden 1982; Twyford 1997). Although variation in density is often limited within local areas due to similarity in available resources (Brown 1995; Rosenzweig 1995), the study areas in the present work were large and encompassed up to 3000 km². It is more likely that the sites within each study area were set within a relatively narrow range of the available vegetation types, and that this restricted the range of abundances observed. For example, no sites were established in highly modified woodland, pasture, swamp or riparian habitats, even though one or more of these additional vegetation types were present in each study area beyond those actually sampled.

Differences in numbers of the three species between sites within each study area were associated most strongly with particular habitat components. The regression equations for all species accounted for some 40–80% of the variance in their numbers, suggesting moderate to good fits of the data. For both *A. agilis* and *A. stuartii*, tree hollows were consistently important, with numbers of logs, invertebrates and *R. fuscipes* explaining further variation in abundance in three of the four study areas. The strong association of *Antechinus* spp. with tree hollows has been identified previously (e.g. Golding 1979; Dickman 1991); animals use hollows for nesting, nurturing of young, sheltering from extremes of weather and from predators, foraging, mating and, probably, lekking (Dickman 1982; 1991; Lazenby-Cohen and Cockburn 1991; Cockburn and Lazenby-Cohen 1992; Ward 2000; see also Table 2 and Fig. 4). There is also some evidence that addition of artificial nests can increase numbers of *A. stuartii* (Cox 2003).

The association of *A. stuartii* with logs in the Blue Mountains probably reflects the preference of this species for dense cover at ground level (Catling and Burt 1995; Catling and Coops 1999; Knight and Fox 2000). It is possible that logs were less important in the other study areas if alternative

ground-level habitat components provided sufficient cover; conversely, the inconsistent association of *A. stuartii* with logs may reflect the semi-arboreal habits of this species (Cox *et al.* 2003; Tasker and Dickman 2004). It is tempting to explain the association of *A. stuartii* with *R. fuscipes* at Ku-ring-gai as being the result of shared preferences for dense ground-level cover. Although rats were not entered into regression equations in other areas, the numbers of these species were correlated positively in Chichester National Park, as were those of *A. agilis* and *R. fuscipes* in the Brindabella Range. The additional association of *A. agilis* with abundance of invertebrates in the Brindabellas may reflect the fact that this species was sampled during a period of drought when food was limited (Dickman 1986b, 1989). The correlation between abundance of *A. stuartii* and invertebrates in the Blue Mountains may also reflect a response to food resources; although FOODNO was not entered into the final regression equation, *A. stuartii* appears to be food-limited in winter in the Blue Mountains and individuals gained mass when provided with supplementary food (Banks and Dickman 2000).

The abundance of *R. fuscipes* also was correlated with logs and the index of tree hollows, but showed additional associations with leaf litter and measures of vegetation cover. These findings broadly parallel those of Barnett *et al.* (1978), Fox and McKay (1981), Lunney *et al.* (1987), Cox *et al.* (2003) and Tasker and Dickman (2004) from other areas. Logs are often used by rats for shelter by day (Table 2) and for cover and foraging by night (Stewart 1979; Dickman 1991), whereas tree hollows appear to be seldom exploited. Adult *R. fuscipes* are poor climbers and probably cannot ascend to hollows in the canopy; it is noteworthy that all hollows observed to be used in this study were in decaying stags no more than 2.6 m above ground. In addition, the association of *R. fuscipes* with the index of tree hollows was positive in the Chichester study area but negative at Ku-ring-gai. Clearly, hollows are not required consistently by this species, and apparent associations may reflect responses by rats to habitat components correlated with hollows such as loose bark or leaf litter.

Rattus fuscipes often appears to avoid dense vegetation in the layer 0–30 cm above ground (Moro 1991; Tasker and Dickman 2004), perhaps because it impedes movement at ground level. This was the case in the Ku-ring-gai study area (Table 1). However, this species generally responds strongly to overall vegetation complexity (Stewart 1979; Catling and Burt 1995; Tasker and Dickman 2004), and in this study was associated with vegetation 26–50 cm above ground in the Blue Mountains and under 1 m in the Brindabellas (Table 1). Vegetation in these layers provides diurnal shelter (Table 2), protection from avian predators and probably access to green plant foods, fruits, fungi and invertebrates. In general, Bush Rats appeared to be associated with similar environmental attributes between study areas, even if different combinations of variables contributed to regression models. Some inconsistency in response can always be expected due to the complexities that are inherent in quantifying environmental variation as it may be perceived by a target species, as well as to variation that is likely at different times or in different parts of its range (Cox *et al.* 2003).



Figure 4. Female Agile Antechinus *Antechinus agilis* returning to her nest site in a tree hollow, with three dependent juveniles clinging to her nipples. (Photo: Chris Dickman)

Are common species important?

So far, we have presented and interpreted the results of this study in a traditional manner, using a suite of independently-measured variables to explain and predict site-based differences in numbers of the three study species. It would be conventional next to use the results to call for management regimes that retain and maximize tree hollows, logs and other important habitat components. Indeed, such calls have been made cogently and eloquently already (e.g. Lindenmayer *et al.* 1990; Recher 1996; Gibbons and Lindenmayer 2002), and we echo and support the arguments. Taken as they are, however, our results are unlikely to be viewed as compelling because *Antechinus* species and *R. fuscipes* are widespread and often abundant in forest habitats in eastern Australia. Given that they are ubiquitous, able

to persist in a wide variety of forest types and are of no current conservation concern, should such species be considered 'important' by forest managers, or should they be dismissed as being of little consequence?

In an ecological sense, common species should be generally important in natural systems. Their abundance ensures that they acquire and control more energy, nutrients and other resources than rare species; direct biotic interactions such as competition, predation and facilitation are likely to be more intense due to frequency-dependent effects (Dickman 2003); indirect interactions such as those occurring within food webs may be enhanced; and co-evolutionary relationships among taxa also should be more complex and developed if the interacting species have been common for many generations (Evans and Schmidt 1990). As common species are seldom equally

abundant throughout their geographical ranges, we might expect that control of resources and the complexity of interactions would be greater in density 'hotspots' than in places of scarcity across the landscape. From the perspective of a researcher, the ability to design adequately replicated studies that yield statistically robust results, such as relating numbers to particular habitat components or combinations of components, is a further practical reason for studying common species. This point has been made in reviews of the status of rodents and dasyurids in New South Wales (Dickman *et al.* 2000, 2001). The numerical advantage of using common species can in turn provide further research opportunities, and hence expand the scope of the questions asked.

In eastern Australia, sites with locally dense populations of *A. agilis* and *A. stuartii* will contain diverse and abundant assemblages of invertebrates that comprise prey for these predatory species (Fox and Archer 1984; Dickman 1991; Lunney *et al.* 2001). Populations of *R. fuscipes* are usually sustained in part by invertebrates, although fungi, seeds and green plant material also form part of the diet. All species visit flowers and carry pollen, while *R. fuscipes* likely acts as a vector also for movement of mycorrhizal spores (Tory *et al.* 1997). The three species also form part of the diet of forest owls (Davey 1993; Kavanagh 1997, 2002) and other native predators, at times suffering intense predation (Lazenby-Cohen and Cockburn 1993). Due to the association of the three species with tree hollows, logs and other habitat components in forest environments, sites with dense populations are likely to be structurally complex and less disturbed by processes such as grazing and burning (Tasker and Dickman 2004). Such sites also are likely to be favoured by less common species with similar shelter requirements (e.g. Dusky Antechinus *Antechinus swainsonii*, Fawn-footed Melomys *Melomys cervinipes*, Tasker and Dickman 2004), including many of the more than 300 species of vertebrates identified by Gibbons and Lindenmayer (2002) that use tree hollows.

In view of the above observations, we suggest that common species could play a uniquely important role in

forest management by helping to identify systems that are resource-rich, complex, sustain webs of species interactions, and are moderately intact. Thus, in a large regional area, sites containing high densities of Bush Rats and antechinuses should arguably be viewed as being of higher 'quality', and overall conservation value, than low density sites. Such sites should also be easy to monitor. Quantitative applications of the precautionary principle in forest management rely on accurate identification of declines in indicator species, and these should be more readily detected in common rather than rare species (Calver *et al.* 1999; Di Stefano 2001). The indexing role of common species often cannot be played by threatened species, despite the attention that such taxa receive from researchers and managers. In part, this is because the habitat and resource requirements of threatened species are usually poorly-known or contentious (Pyke and Read 2002; Meek *et al.* 2003). Different threatened species also do not select the same habitats even when their requirements are known and, because most are scarce throughout their ranges, the discovery of one or a few individuals at any site may be due as much to chance as to the necessary suite of resources being present. Common species might also be useful as 'umbrella species' whose requirements encompass the needs of rare or cryptic taxa that are otherwise difficult to monitor, or as members of 'focal species' groups which collectively indicate landscape quality, particular resources or threats (Lambeck 1997).

In making these points, we do not advocate in any way diminishing or abandoning targeted research and surveys on threatened species. Such work will be essential in continuing to inform and direct forest management in future. We suggest simply that common species can be used to obtain a quick and ready index of forest quality. Other authors have made similar suggestions for other taxa (e.g. McLaren *et al.* 1998; Pharo *et al.* 2000). In future studies, it would be of value to compare an index of forest quality based on the local abundance of common species with more traditional indicators such as richness of different target (including threatened) species, or presence of old-growth trees and other structure-based indicators (Lindenmayer *et al.* 2000), to evaluate the sensitivity and effectiveness of each.

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References

- Banks, P. B. and Dickman, C. R. 2000. Effects of winter food supplementation on reproduction, body mass, and numbers of small mammals in montane Australia. *Canadian Journal of Zoology* 78: 1775-1783.
- Barnett, J. L., How, R. A. and Humphreys, W. F. 1978. The use of habitat components by small mammals in eastern Australia. *Australian Journal of Ecology* 3: 277-285.
- Bausell, R. B. and Li, Y.-F. 2002. *Power Analysis for Experimental Research*. Cambridge University Press: Cambridge.
- Benson, D. H. and Howell, J. (1990). Sydney's vegetation 1788-1988: utilization, degradation and rehabilitation. *Proceedings of the Ecological Society of Australia* 16: 115-127.
- Bradford, S.L. 1976. The vegetation of Ku-ring-gai Chase National Park, Sydney. Honours thesis, University of New South Wales: Sydney.

- Brown, J. H.** 1995. *Macroecology*. University of Chicago Press: Chicago.
- Bureau of Meteorology.** 1988. *Climatic Averages Australia*. Australian Government Publishing Service: Canberra.
- Calver, M. C., Bradley, J. S. and Wright, I. W.** 1999. Towards scientific contributions in applying the precautionary principle: an example from southwestern Australia. *Pacific Conservation Biology* 5: 63-72.
- Catling, P. C. and Burt, R. J.** 1995. Studies of the ground-dwelling mammals of eucalypt forests in south-eastern New South Wales: the effect of habitat variables on distribution and abundance. *Wildlife Research* 22: 271-288.
- Catling, P. C. and Coops, N. C.** 1999. Prediction of the distribution and abundance of small mammals in the eucalypt forests of south-eastern Australia from airborne videography. *Wildlife Research* 26: 641-650.
- Cockburn, A. and Lazenby-Cohen, K. A.** 1992. Use of nest trees by *Antechinus stuartii*, a semelparous lekking marsupial. *Journal of Zoology* 226: 657-680.
- Cornish, P. M.** 1993. The effects of logging and forest regeneration on water yields in a moist eucalypt forest in New South Wales, Australia. *Journal of Hydrology* 150: 301-322.
- Cox, M. P. G.** 2003. The effects of rainforest fragmentation on non-flying mammals on the eastern Dorrigo Plateau, New South Wales, Australia. PhD thesis, University of Sydney: Sydney.
- Cox, M. P., Dickman, C. R. and Hunter, J.** 2003. Effects of rainforest fragmentation on non-flying mammals of the eastern Dorrigo Plateau, Australia. *Biological Conservation* 115: 175-189.
- Davey, S. M.** 1993. Notes on the habitat of four Australian owl species. Pp.126-142 in *Australian Raptor Studies*, edited by P. Olsen. Australasian Raptor Association: Moonee Ponds, Victoria.
- Dickman, C. R.** 1980. Ecological studies of *Antechinus stuartii* and *Antechinus flavipes* (Marsupialia: Dasyuridae) in open-forest and woodland habitats. *Australian Zoologist* 20: 433-446.
- Dickman, C. R.** 1982. Some observations of the behaviour and nest utilization of free-living *Antechinus stuartii* (Marsupialia: Dasyuridae). *Australian Mammalogy* 5: 75-77.
- Dickman, C. R.** 1986a. An experimental study of competition between two species of dasyurid marsupials. *Ecological Monographs* 56: 221-241.
- Dickman, C. R.** 1986b. An experimental manipulation of the intensity of interspecific competition: effects on a small marsupial. *Oecologia* 70: 536-543.
- Dickman, C. R.** 1989. Demographic responses of *Antechinus stuartii* (Marsupialia) to supplementary food. *Australian Journal of Ecology* 14: 387-398.
- Dickman, C. R.** 1991. Use of trees by ground-dwelling mammals: implications for management. Pp. 125-136 in *Conservation of Australia's Forest Fauna*, edited by D. Lunney. Royal Zoological Society of New South Wales: Mosman, NSW.
- Dickman, C. R.** 1996. *Overview of the Impacts of Feral Cats on Australian Native Fauna*. Australian Nature Conservation Agency: Canberra.
- Dickman, C. R.** 2003. Species interactions: direct effects. Pp. 140-157 in *Ecology: An Australian Perspective*, edited by P. Attiwill and B. Wilson. Oxford University Press: Melbourne.
- Dickman, C. R., Green, K., Carron, P. L., Happold, D. C. D. and Osborne, W. S.** 1983. Coexistence, convergence and competition among *Antechinus* (Marsupialia) in the Australian high country. *Proceedings of the Ecological Society of Australia* 12: 79-99.
- Dickman, C. R., Parnaby, H. E., Crowther, M. S. and King, D. H.** 1998. *Antechinus agilis* (Marsupialia: Dasyuridae), a new species from the *A. stuartii* complex in south-eastern Australia. *Australian Journal of Zoology* 46: 1-26.
- Dickman, C. R., Lunney, D. and Matthews, A.** 2000. Ecological attributes and conservation of native rodents in New South Wales. *Wildlife Research* 27: 347-355.
- Dickman, C. R., Lunney, D. and Matthews, A.** 2001. Ecological attributes and conservation of dasyurid marsupials in New South Wales, Australia. *Pacific Conservation Biology* 7: 124-133.
- Di Stefano, J.** 2001. Power analysis and sustainable forest management. *Forest Ecology and Management* 154: 141-153.
- Eby, P. and Lunney, D. (eds)** 2002. *Managing the Grey-headed Flying-fox as a Threatened Species in New South Wales*. Royal Zoological Society of New South Wales: Mosman, NSW.
- Evans, D. L. and Schmidt, J. O. (eds)** 1990. *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators*. State University of New York Press: New York.
- Facey, A. B.** 1981. *A Fortunate Life*. Penguin Books: Camberwell, Victoria.
- Fairley, A.** 1976. *A Field Guide to the National Parks of New South Wales*. Rigby: Adelaide.
- Ferrier, S. and Watson, G.** 1997. *An Evaluation of the Effectiveness of Environmental Surrogates and Modelling Techniques in Predicting the Distribution of Biological Diversity*. Environment Australia: Canberra.
- Fox, B. J. and Archer, E.** 1984. The diets of *Sminthopsis murina* and *Antechinus stuartii* (Marsupialia: Dasyuridae) in sympatry. *Australian Wildlife Research* 11: 235-248.
- Fox, B. J. and McKay, G. M.** 1981. Small mammal responses to pyric successional changes in eucalypt forest. *Australian Journal of Ecology* 6: 29-41.
- Fraser, L. and Vickery, J. W.** 1937. The ecology of the upper Williams River and Barrington Tops districts. *Proceedings of the Linnean Society of New South Wales* 62: 269-283.
- Frawley, K. J. and Semple, N. M. (eds)** 1988. *Australia's Ever Changing Forests: Proceedings of the First National Conference on Australian Forest History*. Department of Geography and Oceanography, Australian Defence Force Academy: Campbell, Canberra.
- Frith, H. J.** 1973. *Wildlife Conservation*. Angus and Robertson: Sydney.
- Gibbons, P. and Lindenmayer, D.** 2002. *Tree Hollows and Wildlife Conservation in Australia*. CSIRO Publishing: Melbourne.
- Golding, B. G.** 1979. Use of artificial hollows by mammals and birds in the Wombat Forest, Daylesford, Victoria. Master of Environmental Science thesis, Monash University: Melbourne.
- Hall, S. and Lee, A. K.** 1982. Habitat use by two species of *Antechinus* and *Rattus fuscipes* in tall open forest in southern Victoria. Pp. 209-220 in *Carnivorous Marsupials*, edited by M. Archer. Royal Zoological Society of New South Wales: Mosman, NSW.
- Hrdina, F.** 1997. Marsupial destruction in Queensland 1877-1930. *Australian Zoologist* 30: 272-286.
- Hunter, M. L.** 1990. *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice-Hall: Englewood Cliffs, New Jersey.
- Kavanagh, R. P.** 1991. The target species approach to wildlife management: gliders and owls in the forests of southeastern New

- South Wales. Pp. 377-383 in *Conservation of Australia's Forest Fauna*, edited by D. Lunney. Royal Zoological Society of New South Wales: Mosman, NSW.
- Kavanagh, R. P. 1997.** Ecology and management of large forest owls in south-eastern Australia. PhD thesis, University of Sydney: Sydney.
- Kavanagh, R. P. 2002.** Comparative diets of the Powerful Owl (*Ninox strenua*), Sooty Owl (*Tyto tenebricosa*) and Masked Owl (*Tyto novaehollandiae*) in southeastern Australia. Pp. 175-191 in *Ecology and Conservation of Owls*, edited by I. Newton, R. Kavanagh, J. Olsen and I. Taylor. CSIRO Publishing: Melbourne.
- Kendall, M. 1980.** *Multivariate Analysis*. Charles Griffin & Company: London.
- Knight, E. H. and Fox, B. J. 2000.** Does habitat structure mediate the effects of forest fragmentation and human-induced disturbance on the abundance of *Antechinus stuartii*? *Australian Journal of Zoology* **48**: 577-595.
- Krebs, C. J. 1989.** *Ecological Methodology*. Benjamin/Cummings: Menlo Park, California.
- Lambeck, R. J. 1997.** Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* **11**: 849-856.
- Lamoreux, J., Akçakaya, H. R., Bennun, L., Collar, N. J., Boitani, L., Brackett, D., Bräutigam, A., Brooks, T. M., da Fonseca, G. A. B., Mittermeier, R. A., Rylands, A. B., Gärdenfors, U., Hilton-Taylor, C., Mace, G. M., Stein, B. A. and Stuart, S. 2003.** Value of the IUCN Red List. *Trends in Ecology and Evolution* **18**: 214-215.
- Lazenby-Cohen, K. A. and Cockburn, A. 1991.** Social and foraging components of the home range in *Antechinus stuartii* (Dasyuridae: Marsupialia). *Australian Journal of Ecology* **16**: 301-307.
- Lazenby-Cohen, K. A. and Cockburn, A. 1993.** Intense predation by owls on lekking Brown Antechinus *Antechinus stuartii*. Pp. 175-180 in *Australian Raptor Studies*, edited by P. Olsen. Australasian Raptor Association: Moonee Ponds, Victoria.
- Lindenmayer, D. B., Cunningham, R. B., MacGregor, C., Tribolet, C. R. and Donnelly, C. F. 2001.** The Nannangrove landscape experiment – baseline data from mammals, reptiles and nocturnal birds. *Biological Conservation* **101**: 157-169.
- Lindenmayer, D. B., Cunningham, R. B., Tanton, M. T. and Smith, A. P. 1990.** The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia, I. Factors affecting the occupancy of trees with hollows. *Biological Conservation* **54**: 111-131.
- Lindenmayer, D. B. and Franklin, J. F. 2002.** *Conserving Forest Biodiversity: a Comprehensive Multiscaled Approach*. Island Press: Washington, D.C.
- Lindenmayer, D. B., Margules, C. R. and Botkin, D. B. 2000.** Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* **14**: 941-950.
- Lunney, D. 1991a.** The future of Australia's forest fauna. Pp. 1-24 in *Conservation of Australia's Forest Fauna*, edited by D. Lunney. Royal Zoological Society of New South Wales: Mosman, NSW.
- Lunney, D. (ed.) 1991b.** *Conservation of Australia's Forest Fauna*. Royal Zoological Society of New South Wales: Mosman, NSW.
- Lunney, D. (ed.) 2004.** *Conservation of Australia's Forest Fauna* (second edition). Royal Zoological Society of New South Wales: Mosman, NSW.
- Lunney, D., Cullis, B. and Eby, P. 1987.** Effects of logging and fire on small mammals in Mumbulla State Forest, near Bega, New South Wales. *Australian Wildlife Research* **14**: 163-181.
- Lunney, D., Matthews, A. and Grigg, J. 2001.** The diet of *Antechinus agilis* and *A. swainsonii* in unlogged and regenerating sites in Mumbulla State Forest, south-eastern New South Wales. *Wildlife Research* **28**: 459-464.
- Maitz, W. E. and Dickman, C. R. 2001.** Competition in two species of native Australian *Rattus*: is competition intense, or important? *Oecologia* **128**: 526-538.
- Marlow, B. J. 1958.** A survey of the marsupials of New South Wales. *CSIRO Wildlife Research* **3**: 71-114.
- Marzluff, J. M. 1984.** Assumptions and design of regression experiments: the importance of lack-of-fit testing. Pp. 165-171 in *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*, edited by J. Verner, M. L. Morrison and C. J. Ralph. University of Wisconsin Press: Wisconsin.
- McComb, W. and Lindenmayer, D. B. 1999.** Dying, dead, and down trees. Pp. 335-372 in *Maintaining Biodiversity in Forest Ecosystems*, edited by M. L. Hunter, Jr. Cambridge University Press: Cambridge.
- McLaren, M. A., Thompson, I. D. and Baker, J. A. 1998.** Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. *Forest Chronology* **74**: 241-248.
- Meek, P. D., McCray, K. and Cann, B. 2003.** New records of Hastings River Mouse *Pseudomys oralis* from State Forest of New South Wales pre-logging surveys. *Australian Mammalogy* **25**: 101-105.
- Milledge, D. R., Palmer, C. L. and Nelson, J.L. 1991.** "Barometers of change": the distribution of large owls and gliders in Mountain Ash forests of the Victorian Central Highlands and their potential as management indicators. Pp. 53-65 in *Conservation of Australia's Forest Fauna*, edited by D. Lunney. Royal Zoological Society of New South Wales: Mosman, NSW.
- Moro, D. 1991.** The distribution of small mammal species in relation to heath vegetation near Cape Otway, Victoria. *Wildlife Research* **18**: 605-618.
- Pharo, E. J., Beattie, A. J. and Pressey, R. L. 2000.** Effectiveness of using vascular plants to select reserves for bryophytes and lichens. *Biological Conservation* **96**: 371-378.
- Possingham, H. P., Andelman, S. J., Burgman, M. A., Medellin, R. A., Master, L. L. and Keith, D. A. 2002.** Limits to the use of threatened species lists. *Trends in Ecology and Evolution* **17**: 503-507.
- Pyke, G. H. and Read, D. G. 2002.** Hastings River Mouse *Pseudomys oralis*: a biological review. *Australian Mammalogy* **24**: 151-176.
- Quinn, G. P. and Keough, M. J. 2002.** *Experimental Design and Data Analysis for Biologists*. Cambridge University Press: Cambridge.
- Recher, H. F. 1996.** Conservation and management of eucalypt forest vertebrates. Pp. 339-388 in *Conservation of Faunal Diversity in Forested Landscapes*, edited by R. M. DeGraaf and R. I. Miller. Chapman & Hall: London.
- Recher, H. F., Rohan-Jones, W. and Smith, P. 1980.** *Effects of the Eden Woodchip Industry on Terrestrial Vertebrates with Recommendations for Management*. Forestry Commission of New South Wales: Sydney.
- Reed, P. 1991.** An historical analysis of the changes to the forests and woodlands of New South Wales. Pp. 393-406 in *Conservation of Australia's Forest Fauna*, edited by D. Lunney. Royal Zoological Society of New South Wales: Mosman, NSW.

- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press: Cambridge.
- Specht, R. L. 1970. Vegetation. Pp. 44-67 in *The Australian Environment*, edited by G. W. Leeper. CSIRO and Melbourne University Press: Melbourne.
- Statham, H. L. 1982. *Antechinus stuartii* (Dasyuridae, Marsupialia) diet and food availability at Petroi, northeastern New South Wales. Pp. 151-163 in *Carnivorous Marsupials*, edited by M. Archer. Royal Zoological Society of New South Wales: Mosman, NSW.
- Statham, H. L. and Harden, R. H. 1982. Habitat utilization of *Antechinus stuartii* (Marsupialia) at Petroi, northern New South Wales. Pp. 165-185 in *Carnivorous Marsupials*, edited by M. Archer. Royal Zoological Society of New South Wales: Mosman, NSW.
- Steeves, T. E. 1990. The ecology and habitat use of two species of small mammals, the Brown Antechinus (*Antechinus stuartii*) and the Southern Bush Rat (*Rattus fuscipes*). Honours thesis, University of Sydney: Sydney.
- Stewart, A. P. 1979. Trapping success in relation to trap placement with three species of small mammals, *Rattus fuscipes*, *Antechinus swainsonii* and *A. stuartii*. *Australian Wildlife Research* 6: 165-172.
- Tabachnick, B. and Fidell, L. 1996. *Using Multivariate Statistics*, 3rd edition. Harper & Row: New York.
- Tasker, E. M. and Dickman, C. R. 2002. A review of Elliott trapping methods for small mammals in Australia. *Australian Mammalogy* 23: 77-87.
- Tasker, E. M. and Dickman, C. R. 2004. Small mammal community composition in relation to cattle grazing and associated burning in eucalypt forests of the northern tablelands of New South Wales. Pp. 721-40 *Conservation of Australia's Forest Fauna* (second edition), edited by D. Lunney. Royal Zoological Society of New South Wales: Mosman, NSW.
- Thomas, J. and Benson, D. H. 1985. *Vegetation of Ku-ring-gai Chase National Park and Muogamarra Reserve*. National Herbarium of New South Wales, Royal Botanic Gardens: Sydney.
- Tory, M. K., May, T. W., Keane, P. J. and Bennett, A. F. 1997. Mycophagy in small mammals: a comparison of the occurrence and diversity of hypogeal fungi in the diet of the Long-nosed Potoroo *Potorous tridactylus* and the Bush Rat *Rattus fuscipes* from southwestern Victoria, Australia. *Australian Journal of Ecology* 22: 460-470.
- Troughton, E. 1957. *Furred Animals of Australia*. 6th edition. Angus and Robertson: Sydney.
- Twyford, K. L. 1997. Habitat relationships of small mammals at Port Campbell National Park, Victoria. *Australian Mammalogy* 20: 89-98.
- Tyndale-Biscoe, C. H. and Calaby, J. H. 1975. Eucalypt forests as refuge for wildlife. *Australian Forestry* 38: 117-133.
- Ward, S. J. 2000. Possible predation on Feathertail Gliders (*Acrobates pygmaeus*) by Agile Antechinus (*Antechinus agilis*). *Australian Mammalogy* 21: 173-176.
- Warneke, R. M. 1971. Field study of the Bush Rat. *Wildlife Contributions Victoria* 14: 1-115.
- Warneke, R. M. 1978. The status of the Koala in Victoria. Pp. 109-114 in *The Koala: Proceedings of the Taronga Symposium on Koala Biology, Management and Medicine*, edited by T. J. Bergin. Zoological Parks Board of New South Wales: Sydney.
- Whelan, R. J., Ward, S., Hogbin, P. and Wasley, J. 1996. Responses of heathland *Antechinus stuartii* to the Royal National Park wildfire in 1994. *Proceedings of the Linnean Society of New South Wales* 116: 97-108.
- Wilson, B. A., Bourne, A. R. and Jessop, R. E. 1986. Ecology of small mammals in coastal heathland at Anglesea, Victoria. *Australian Wildlife Research* 13: 397-406.
- Wood, D. H. 1971. The ecology of *Rattus fuscipes* and *Melomys cervinipes* (Rodentia: Muridae) in a southeast Queensland rainforest. *Australian Journal of Zoology* 19: 371-392.